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Contrasting effects of fog frequency on the radial growth of two tree species in a Mediterranean-temperate ecotone

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ABSTRACT

The performance and persistence of rear-edge tree populations are relevant issues for conserving biodiversity because these stands harbor high intraspecific biodiversity and play a key role during periods of climate change. The occurrence of these populations is associated with the influence of heterogeneous topography, creating suitable refugia with regionally rare environmental conditions. Climate is changing at a global-scale, but little is known about the long-term impact on local climatic singularities and the associated taxa. We analyzed tree-ring growth chronologies of the two species (*Fagus sylvatica* and *Quercus ilex*) forming the evergreen-deciduous forest ecotone, constitutive of the rear-edge of *F. sylvatica* distribution. The study area is a coastal range with frequent fog immersion, which has been hypothesized to favor the persistence of *F. sylvatica* in Mediterranean peninsulas. We analyzed the long-term effect of fog on tree growth along a topographical gradient and the sensitivity of growth to rainfall and temperature. The annual number of foggy days has decreased by 62% over the last four decades, concomitant with increasing temperatures. Fog frequency was a relevant factor determining tree growth; fog during summer had positive effects on *F. sylvatica* growth mainly through a temperature buffering effect. The positive effect of fog on the growth of *Q. ilex*, however, was likely caused by a collinearity with rainfall. *Q. ilex* growth was less sensitive to climate than *F. sylvatica*, but growth of both species was enhanced by a positive early-summer water balance. Our results indicate that a decrease in fog frequency and an increase in temperature may generally benefit *Q. ilex* in this forest ecotone. Although future changes in rainfall and temperature matter most for the fate of rear-edge tree populations, local climatic singularities such as fog should also be considered. Those can have complementary effects that can swing the balance in ecotones and rear-edge tree populations such as those studied here.

1. Introduction

The distribution of tree species is strongly determined by climate, so the ongoing climatic warming is expected to cause range shifts both upward and poleward (Jump et al., 2009). Upslope range shifts of tree species have already been observed in mid-latitudes (Penuelas and Boada, 2003; Camarero, 2004; Lenoir et al., 2008). Latitudinal range shifts, however, would require tree species to migrate and colonize at distances a thousand-fold larger than for altitudinal ascents (Jump et al., 2009). Large-scale studies using data from forest inventories have found that latitudinal range contraction is much more usual than range expansion (Zhu et al., 2012), and species distribution models suggest that tree species will not be able to migrate to distances fast enough to track the pace of climate change (Liang et al., 2016). Tree populations at the rear edge of a species 'distribution (drier and warmer areas) have been hypothesized to be the most likely to disappear or show signs of growth and vigor decline (Piovesan et al., 2008), recruitment failure (Matías and Jump, 2014), and mortality (Camarero et al., 2015a) or by being outcompeted by coexisting species better adapted to the new conditions (Mueller et al., 2005). Rear-edge populations, though, can be as, or even more, resistant to high temperatures and drought than core range populations (Hacket-Pain et al., 2016; Cavin and Jump, 2017).

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Rear-edge tree populations thrive in areas or climatic refugia with heterogeneous topography that provide a great diversity of suitable climatic niches (Hampe and Petit, 2005). Indeed, climate-induced transitions between vegetation types are not only influenced by increasing drought but also notably by topographically dependent variables such as slope, wind and solar radiation (Vidal-Macua et al., 2017). The fate of the distribution of tree species under future climatic conditions will strongly depend on the survival of rear-edge populations, which are in turn influenced by the interactions between climate and topography (Hampe and Petit, 2005). The quantification of the effects of these factors on the performance of rear-edge tree populations is therefore necessary to predict the responses of forests to climate change.

The common beech (*Fagus sylvatica* L.) is a broadleaved deciduous tree widely distributed throughout western and central Europe (Cavin and Jump, 2017). The response of *F. sylvatica* to climate change has been a subject of numerous studies across its distribution and of recent range-wide assessments because of its importance for forestry (see among others Hacket-Pain et al. (2016) and Cavin and Jump (2017)). Studies focused on particular populations along the southern edge of the distribution of *F. sylvatica* have reported decreases in radial growth (Jump et al., 2006), reduced recruitment (Peñuelas et al., 2007) and high sensitivity to dry and warm summers (Dorado-Liñán et al., 2017; Sánchez de Dios et al., 2016; Tegel et al., 2014). Paradoxically, *F. sylvatica* is the most abundant deciduous broadleaved species in its southwestern distributional limit, and its distribution area is expanding owing to biotic and land use factors (Sánchez de Dios et al., 2016). Long-term increases in basal-area increment have similarly been reported for rear-edge populations in the Italian peninsula (Tognetti et al., 2014). Therefore, finding a common pattern of response of the rear-edge populations of *F. sylvatica* to a warmer and drier climate has not been possible. Tree populations can differ widely in their sensitivity to climate, even at the regional level (Di Filippo et al., 2007; Rozas et al., 2015). Patterns of atmospheric circulation in combination with rough topography can produce contrasting climatic constraints among populations separated by tens of kilometers. Importantly, frequent fog immersion linked to particular atmospheric patterns may weaken the strong dependence of tree growth on summer rainfall (Rozas et al., 2015). Large uncertainties in the response of *F. sylvatica* to climate at the regional level will inhibit understanding at a finer spatial scale. Tree populations can nonetheless survive in geographically isolated climatic refugia containing only a few hundred individuals (Hampe and Jump, 2011). Small populations, aided by particular physiographic conditions, can persist for tens of millennia (Lafontaine et al., 2014). Micro-environments created by unusually moist conditions could effectively delay or buffer the retraction of *F. sylvatica* populations in the face of climate change. Understanding the effects of small-scale topographical gradients on the sensitivity of tree populations to climate is thus needed.

The persistence of rear-edge tree populations is likely to be affected not only by climate and topography, but also by the competitive interactions with the surrounding communities (Hampe and Petit, 2005). A potential retraction of *F. sylvatica* could thus be accelerated by improvements of demographic rates (growth, recruitment or mortality) of neighboring species in response to climate change. Southern, rear-edge populations of *F. sylvatica* are in contact with evergreen Mediterranean vegetation (Jump et al., 2007). *F. sylvatica* tends to occur in mountainous areas and north-facing slopes (Cavin and Jump, 2017) and so commonly occupies the moister sites and higher altitudes, whereas evergreen vegetation occupies mainly lower areas and south-facing slopes (de Bolòs, 1983; Penuelas and Boada, 2003; Peñuelas et al., 2007; Barbeta and Peñuelas, 2017). Growth rates of evergreen species have increased in the ecotone between these two vegetation types in recent decades (Barbeta and Peñuelas, 2017). More drought-resistant evergreen species such as the Holm oak (*Quercus ilex* L.) may thus be favored by ongoing climatic shifts and may progressively replace broadleaved deciduous species. The location of the ecotone between deciduous and evergreen forests has traditionally been attributed to the mean altitude of fog formation at some sites (de Bolòs, 1983; Gutiérrez, 1988). Fog may thus be critical for the occurrence of broadleaved deciduous but not evergreen forests. Indeed, the growth of beech stands in coastal areas is positively influenced by cloudiness during the growing season (Rozas et al., 2015). Fog may mitigate drought stress in many forest ecosystems by reducing vapor-pressure deficits (Limm et al., 2009; Simonin et al., 2009) and may even effectively serve as a water source to trees (Berry et al., 2014). Changes in the frequency of fog may thus likely have an impact on tree growth. Upslope fog formation, however, is strongly dependent on topography and exposure to sea breezes (Cereceda et al., 2002; Scholl et al., 2011), so the effect of fog on tree growth and ecotonal dynamics can differ at small spatial scales.

We analyzed chronologies of tree-ring growth for the two main species forming the evergreen-deciduous forest ecotone at the southernmost limit of *F. sylvatica* distribution. We assessed the influence of topography by studying four sites with contrasting exposure to sea breezes but sharing the same altitude, aspect and forest composition. A unique 44-yr long series of fog incidence was used to quantify the influence of fog on tree-ring growth. In particular, we (a) analyzed the long-term patterns in fog frequency, (b) assessed the role of topography in mediating the climatic sensitivity of the Mediterranean temperate forest ecotone and (c) determined the influence of changing temperature, rainfall and fog frequency on the patterns of growth. We hypothesized that the growth of the temperate deciduous tree *F. sylvatica* is more sensitive to high temperatures and summer drought, compared to the evergreen Mediterranean *Q. ilex*. More importantly, we tested the hypothesis that fog frequency is beneficial for *F. sylvatica* but not for *Q. ilex*, and the effect of fog on growth is stronger in the sites that are more exposed to sea breezes. Many case studies have reported the importance of fog for forest water budgets (Berry et al., 2014; Eller et al., 2013; Ewing et al., 2009; Goldsmith et al., 2013; Limm et al., 2009; Ritter et al., 2005). Most of these studies, however, were conducted in tropical montane cloud forests or in seasonally dry forests. Fog in temperate, less water-limited ecosystems has rarely been considered as a relevant factor for tree growth (but see Berry et al. (2014) and Rozas et al. (2015)). The temperature-driven increases in vapor-pressure deficit due to current climate change may enhance the importance of fog for mitigating drought in temperate forests subjected to Mediterranean influence, in addition to the ecosystems currently considered fog-dependent.

2. Material and methods

2.1. Study area

This study was conducted in Montseny Natural Park (Catalonia, Spain, northeastern Iberian Peninsula; 41°49′28″N, 2°24′20″E). This park encompasses a mountain range that reaches 1706 m a.s.l. and is < 20 km from the Mediterranean Sea, which provides moist air from sea breezes (Fig. 1). The altitudinal range of the Montseny Mountains (from 300 to 1706 m) confers a variety of climatic conditions. The lower areas have a humid subtropical climate (*Cfa*, in the Koppen-Geiger classification). Rainfall, however, is highly variable interannually, producing cyclical droughts, notably in summer. The mean annual rainfall is higher in the eastern foothills compared to the western foothills (695 vs 792 mm), and the climate becomes oceanic (*Cfb*) in more elevated areas (de Bolòs, 1983). The highest peak (Turó de l'Home, 1706 m) has a mean annual temperature of 6.9 °C and a mean annual rainfall of 1045 mm. Importantly, this peak is covered by upslope fog with a mean of 212 days per year (1967–2000 data). These mountains are densely forested, although pastures occupy the ridgetops. The forests were intensively managed in the past (logging, coppicing, charcoal production) but have not been managed since the first half of the 20th century (Penuelas and Boada, 2003).

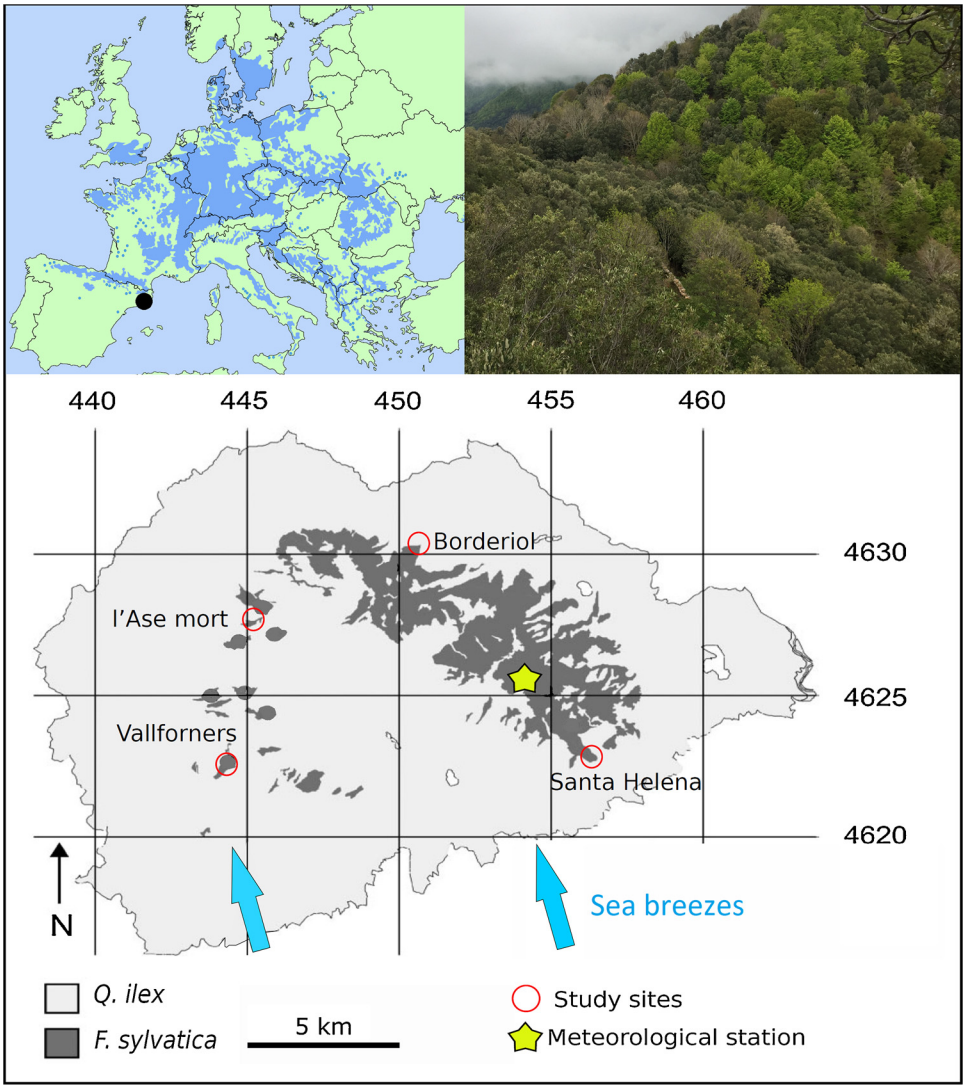

Fig. 1. The upper left panel shows the location of the study area in Europe (black dot) and the distribution of *Fagus sylvatica* in Europe (blue) according to the Euforgen program (http://www.euforgen.org/). The upper right panel is a photograph of the Mediterranean-temperate forest ecotone, formed by *Q. ilex* and *F. sylvatica*, in spring. The lower panel shows the location of each site in the Mediterranean-temperate forest ecotone and the local distributions of the areas dominated by the two studied species (but with minor presence of other species). Grid lines are marked with Universal Transverse Mercator coordinates in kilometers.

The Montseny Mountains harbor one of the southernmost populations of the temperate deciduous *F. sylvatica*, the common beech, in Europe (Fig. 1). *F. sylvatica* is distributed from southern Scandinavia to the mountainous areas of Mediterranean peninsulas. This species dominates the forests at the highest altitudinal range in the Montseny Mountains (750–1690 m a.s.l.). The lower areas of these mountains are covered by Mediterranean evergreen forests, mostly dominated by Holm oak, *Q. ilex* (300–1300 m a.s.l.) (de Bolòs, 1983). Forests of these two dominant species form a marked ecotone (Fig. 1) at an altitude ranging from 800 to 1300 m a.s.l., depending on the aspect. The eastern half of the mountains is considerably higher and thus contains more suitable habitats for *F. sylvatica*, as shown by its local distribution in Fig. 1. Sea breezes from the SSW are frequent in late summer and promote the formation of upslope fog after midday (Fontserè, 1917). The altitude of the cloud is lower on the southern than the northern face of the mountain range, because sea breezes lose moisture as they cross the range (Panareda, 1979). In one of the studied sites (Santa Helena), a daily maximum of 166.8 mm of fog were collected. Fog events appear to leave the highest amounts of water during cyclonic situations (Corell Custardoy et al., 2014). However, advective situations are those who produce most of the fog events, especially when bringing maritime air. In addition, it has been clearly shown that lower areas dominated by *Q. ilex* (ca. 800–900 m) present a much lower fog precipitation amount and frequency than the ecotonal sites studied here (ca. 1100–1200 m) (Corell Custardoy et al., 2014).

The western half of the mountains is lower (highest elevation is Puig Drau, 1344 m a.s.l.) and slightly farther from the coast (Table 1), so upslope fog forms less frequently than on the eastern side. The extent of *F. sylvatica* is restricted on the western side to forest patches in sheltered and north-facing areas (Fig. 1). Past conversion of forest into grasslands, however, may be responsible for the current scattered distribution of *F. sylvatica* in this area (Jump and Peñuelas, 2006; Oliver, 2003). We selected four sites in which *F. sylvatica* and *Q. ilex* forest coexist as representatives of the Mediterranean-temperate ecotone: Borderiol (NE), l'Ase mort (NW), Santa Helena (SE) and Vallforners (SW). These sites were all at the same altitude (1100–1200 m a.s.l.) but were distributed along the two main mountain ranges and at different distances to the sea (Table 1). The nomenclature used for the sites (SW, SE, NW, NE) does not refer to the aspect (which is mostly northerly in all of the sites) but to the relative position within the mountain range. The soils in the study area are Dystric Cambisols and Dystric Regosols established either over granodiorite or schist (Peñuelas et al., 2008).Table 1.

Table 1
Site description and characteristics of the tree-ring chronologies.

Site	Distance to the sea (km)	Aspect	Tree species	Mean DBH ± SE (mm)	Number of trees	Chronology length (years)	Time span	EPS	Mean *rbar* ± SD
Vallforners (SW)	26	N-NW	*F. sylvatica*	441 ± 23	28	133	1882-2015	0.981	0.69 ± 0.11
			Q. ilex	298 ± 9	18	92	1923-2015	0.911	0.49 ± 0.15
Santa Helena (SE)	21	SW-NE	*F. sylvatica*	431 ± 23	20	95	1920-2015	0.950	0.58 ± 0.19
			Q. ilex	300 ± 10	13	77	1938-2015	0.784	0.42 ± 0.16
l'Ase mort (NW)	30	N-NW	*F. sylvatica*	443 ± 27	28	94	1921-2015	0.965	0.58 ± 0.13
			Q. ilex	307 ± 24	11	92	1923-2015	0.757	0.43 ± 0.23
Borderiol (NE)	30	N-W	*F. sylvatica*	351 ± 28	25	86	1925-2011	0.896	0.60 ± 0.1
			Q. ilex	339 ± 10	19	66	1945-2011	0.912	0.55 ± 0.13

Topographic characteristics of the sites and descriptions of the corresponding chronologies for each species. Mean DBH, mean diameter at breast height of the trees; SE, standard error of the mean; EPS, expressed population signal, which evaluates the replication and internal coherence of the chronology or mean site series, and *rbar*, the inter-series correlation

2.2. Climatic data

Climatic data were obtained from the meteorological station on Turó de l'Home, the highest peak (1706 m a.s.l.; 41°46′21″N, 2°26′15″E). This station was closed in 2004, and data from more modern nearby stations were used to reconstruct the series until 2015 (see details below). At the Turó de l'Home station, the daily presence or absence of fog (and other phenomena) has been registered since the 1950s. High-quality data of foggy days spanned 1967-2000. We obtained fog data for 2000–2011 by correlating monthly foggy days recorded on Turó de l'Home with monthly mean relative humidity from a station 10 km away but within the same mountain range (Tagamanent, $R^2 = 0.51$, $P < 0.0001$). Maximum and minimum temperatures and rainfall for 2004–2011 were obtained by correlations ($R^2 = 0.98$, 0.98 and 0.66, respectively) with another meteorological station 7 km away within Montseny Natural Park (Viladrau). The seasonal climate in the station at the highest peak (Turó de l'Home), the station at the NE side of the mountains but lower altitude (Viladrau), and the station at the SW side (Tagamanent), are very similar. The most remarkable difference is the expected temperature difference caused by altitude. The climographs of these three stations are shown in Fig. S2. In addition, in three of the sites (SW, NW and NE), we installed temperature and air relative humidity sensors (EasyLog EL-USB-2, Lascar Electronics, Whiteparish, UK) inside the forest from 2012 and 2014. Finally, monthly and daily values of air relative humidity (Fig. S1) were obtained from a new meteorological station installed 400 m from the old Turó de l'Home station.

2.3. Tree-ring data

Tree cores of *F. sylvatica* and stem disks of *Q. ilex* were sampled in winter 2013, as described by Barbeta and Peñuelas (2017). We randomly selected at least 10–15 dominant or co-dominant trees of the two species. The target areas were the narrow ecotone where both species coexisted. Two to three cores were extracted from each individual at breast height (1.30 m) and perpendicular to the slope with a 4.3-mm increment borer. We also measured the diameter at breast height (DBH). All tree cores were air-dried in the laboratory, mounted on wooden supports and polished with sandpaper of decreasing grit size. Polished *F. sylvatica* cores were scanned at 1200 dpi. The images were used to identify tree-ring boundaries and to measure tree-ring widths using CooRecoder (Cybis Elektronic & Data AB, Saltsjöbaden, Sweden) and a stereomicroscope. Cross-dating was done visually and statistically tested using CDendro (Cybis Elektronic & Data AB, Saltsjöbaden, Sweden) and COFECHA (Grissino-Mayer, 2001; Holmes, 1983), respectively. Tree-ring boundaries were identified, and tree-ring widths were measured with a resolution of 0.01 mm using LINTAB and TSAP-WIN (Rinntech, Heidelberg, Germany). Tree-ring boundaries are difficult to be identified for *Q. ilex*, mainly due to the common presence of false rings or density fluctuations (Gea-Izquierdo et al., 2009). We successfully cross-dated fewer *Q. ilex* than *F. sylvatica* individuals from the same sites but obtained at least 11 individual series for each site. The series of tree-ring widths for each site and species were detrended using negative exponential functions and an autoregressive model in order to focus in the high-frequency variations in tree-ring width by removing low frequency variations related to tree age and size. The resulting individual mean series for a ring-width index (RWI) were averaged to obtain mean chronologies at site and species levels using a Tukey bi-weight robust mean.

A chronology of mean tree-ring widths (in mm) was also calculated for each tree, which was subsequently transformed into yearly basal-area increments (BAIs in mm^2) by subtracting the basal area accumulated during the previous year *t*-1 from the basal area accumulated during year *t* ($BAI_t = \pi R_t^2 - \pi R_{t-1}^2$, where *R* is the tree radius, assuming a circular stem) (Biondi and Qeadan, 2008). The BAI chronologies had an initial phase where growth was suppressed because the trees were not yet dominant. The inflection point where a chronology sharply increased its BAI, reaching dominance after the juvenile phase and thus mature growth, could be identified by calculating a nine-year running mean for BAI (Jump et al., 2006). The mature growth phase was considered as the period following a stabilization of the nine-year running mean trends, accounting for the inter-annual variation range. We assessed the temporal trends in BAI by exclusively using the mature phase of growth of each chronology. Mature growth, however, began in different years in each chronology (*F. sylvatica* tended to be older than *Q. ilex*) due to the diverse age structure of each stand. We also analyzed the trends in BAI for the common period of mature growth (1987–2011) for comparing sites and species with the same climate. Tree-ring widths were detrended and BAIs were calculated using the *dplR* package (Bunn, 2008) in R (R Core Development Team, 2012).

2.4. Statistical analyses

We fitted linear relationships to analyze the temporal trends in several series of annual data: mean temperature, total rainfall and number of foggy days. We similarly analyzed the temporal trends in annual stem growth (BAI) based on the sign of the slope and its significance. Monthly patterns in air relative humidity were compared by ANOVAs and Tukey's post hoc tests. The correlations between the standardized tree-ring chronologies (RWI) and maximum and minimum temperatures, rainfall and fog patterns were calculated using correlation functions in the *dplR* package in R (Bunn, 2008). Correlations were calculated from the previous June to the current September based on previous studies (Rozas et al., 2015). The climatic variables were obtained as described above from the Turó de l'Home meteorological station. The period analyzed (1968–2011) corresponded to the maximum overlapping years with fog and tree-ring data for the four sites. We also performed partial correlations to ensure that potential correlations between climatic variables did not affect the results. Foggy days were correlated with maximum temperatures and rainfall (Fig. S3), so we ran a partial correlation analysis using the *treeclim* package in R (Zang and Biondi, 2015), which could identify collinearity between climatic variables and tree-ring growth. This analysis targeted seasonal correlations using monthly climatic data at intervals of three months. RWI was first correlated with one of the primary variables (rainfall and maximum temperature), and then the residuals of these correlations were subsequently correlated with the secondary variable (monthly fog days). BAI trends were assessed using the average BAI series for each site and species and fitting linear relationships for the period corresponding to mature growth. Finally, we compared the BAIs between species and sites and their trends for the common period of mature growth (1987–2011) using linear relationships and generalized linear mixed models in the *nlme* package in R to account for year as a random factor.

3. Results

Mean annual temperature at the Turó de l'Home meteorological station increased by 0.009 °C per year during 1920–2015 ($P < 0.001$, $R^2 = 0.14$). Mean annual rainfall for the same period did not have a significant trend ($P = 0.95$). The annual number of foggy days decreased sharply by 3.47 days per year for 1967–2015 ($P < 0.0001$, $R^2 = 0.81$), (Fig. 2). Monthly maximum temperatures were negatively correlated with the monthly number of foggy days ($P < 0.001$), and this correlation was stronger in summer (Fig. S3). Monthly number of foggy days was positively correlated with rainfall ($P < 0.001$) but more strongly in summer. Mean monthly air relative humidity varied greatly throughout the year during 2010–2015 (Fig. S1a). Air relative humidity peaked in April and again in late summer and early autumn. The air was drier in early to mid-summer (June-August), but the atmospheric conditions were driest in winter (December-February). Air relative humidity was lowest at 7:00, progressively increased during the day to a maximum around 15:00-16:00 and then decreased and stabilized throughout the night. Data from the sensors inside the forest show that microclimatic differences between sites exist, but they are not remarkable. The seasonal trends in temperature and air relative humidity are coincident (Fig. S4). The western sites have overall more air moisture and slightly cooler temperatures than the NE site, whereas climatic differences in the midday are rather small (Fig. S4).

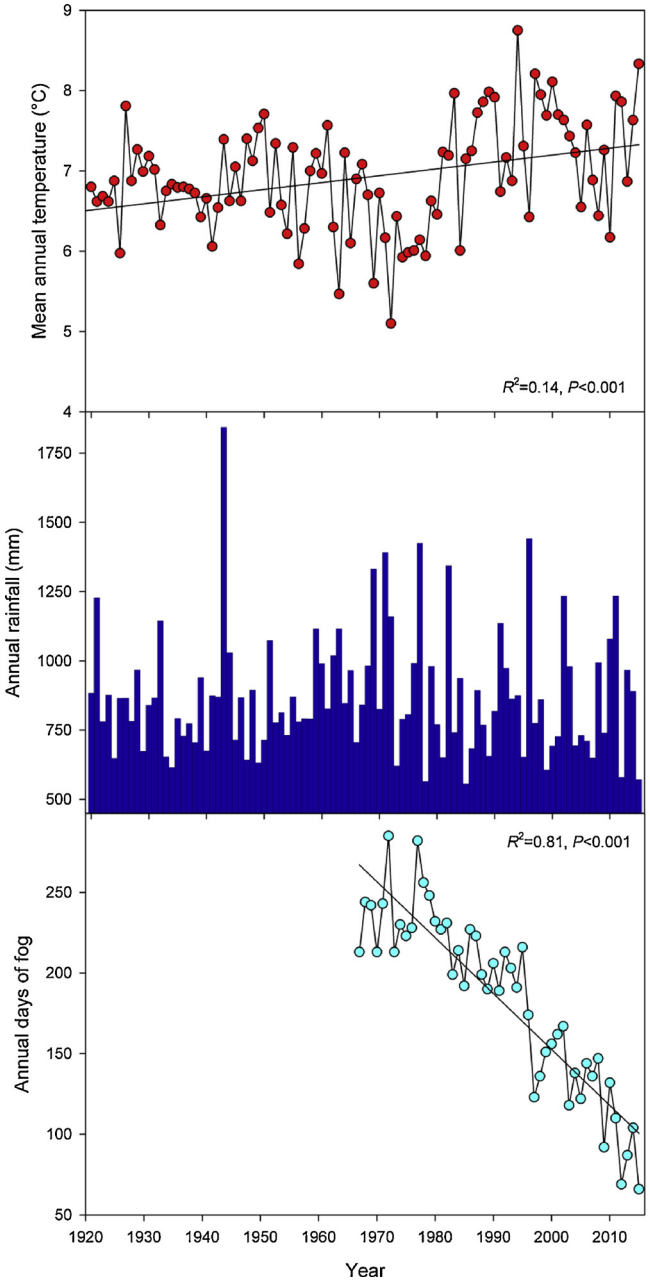

Fig. 2. Temporal variation of climatic variables at the Turó de l'Home meteorological station (1706 m). The upper, middle and lower panels are for mean temperature, rainfall and foggy days, respectively. The series of foggy days starts in 1967, and the other two climatic series start in 1920.

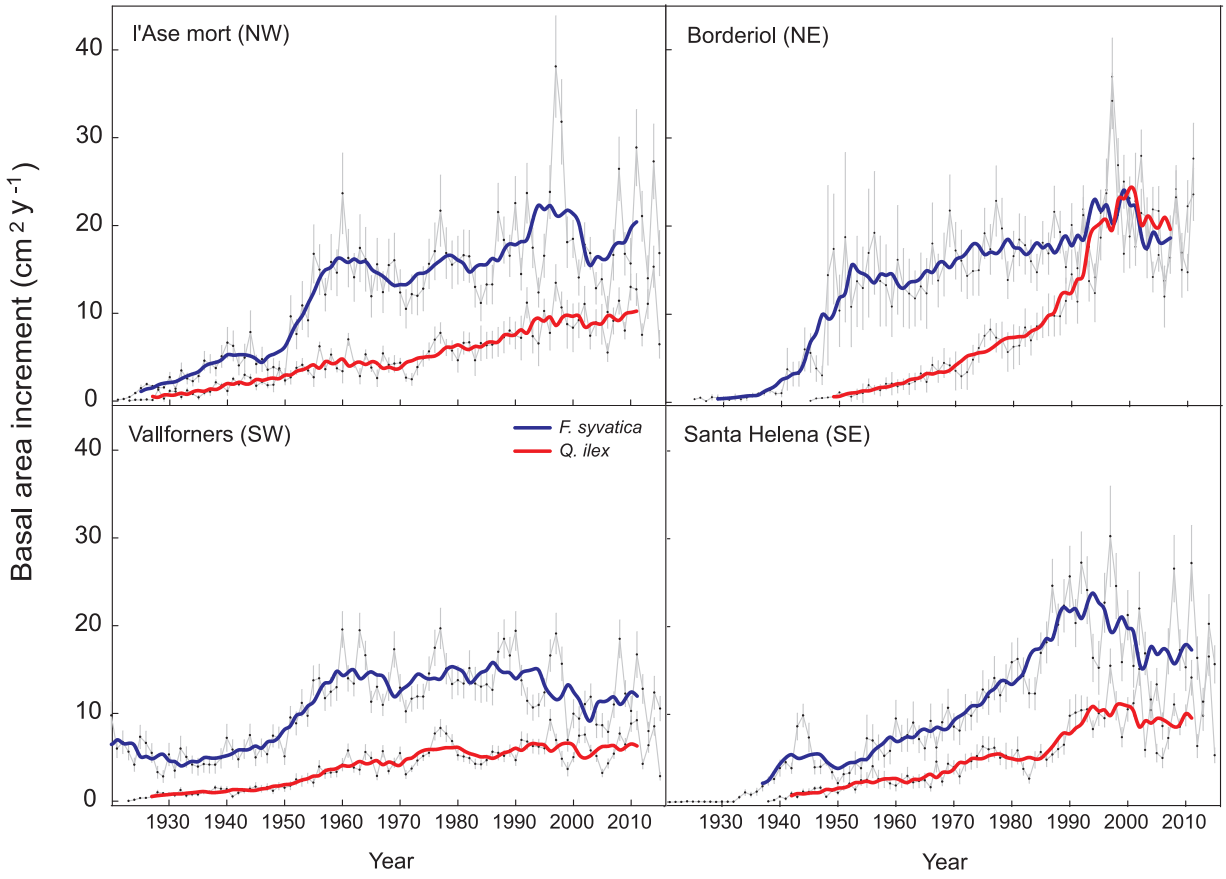

Fig. 3. Basal-area increment (BAI) for each species and site (SE, SW, NE and NW). Gray lines are the annual mean BAIs, and the error bars are standard errors of the means. The colored lines (blue for *F. sylvatica* and red for *Q. ilex*) are the nine-year running mean BAIs.

Table 2
Trend and significance of the long-term growth pattern (BAI, basal-area increment) for each species and site. The first estimates and *P* values correspond to the period of mature growth, which differs for each chronology. The second estimates and *P* values correspond to the period with common mature growth for all chronologies (1987–2011). Significant ($P < 0.05$) BAI trends are shown in bold type.

Site	Species	Onset of mature growth	*Individual period of mature growth*		*Common period of mature growth (1987-2011)*	
			Estimated BAI trend ($cm^2\ y^{-1}$)	*P*	Estimated BAI trend ($cm^2\ y^{-1}$)	*P*
Vallforners (SW)	*F. sylvatica*	1959	**−0.06**	**0.0108**	*−0.1995*	*0.059*
	Q. ilex	1960	**0.035**	**0.0081**	0.046	0.303
Santa Helena (SE)	*F. sylvatica*	1992	−0.03	0.758	*−0.2642*	*0.088*
	Q. ilex	1976	0.053	0.479	0.074	0.37
l'Ase mort (NW)	*F. sylvatica*	1958	**0.105**	**0.0183**	−0.06	0.74
	Q. ilex	1978	**0.138**	**< 0.0001**	**0.1182**	**0.044**
Borderiol (NE)	*F. sylvatica*	1951	**0.122**	**0.0001**	−0.023	0.89
	Q. ilex	1993	0.025	0.915	**0.37**	**0.0224**

Mean BAI for the common period 1987–2011 differed between species and sites (Fig. 3 and Fig. S5). Mean *F. sylvatica* BAI was similar at SE, NE and NW (20.1 ± 1.1, 20.0 ± 1.1 and 19.3 ± 1.3 $cm^2\ y^{-1}$, respectively), but was significantly lower at SW (13.0 ± 0.8 $cm^2\ y^{-1}$, $P < 0.001$). Mean *Q. ilex* BAI was also lowest at SW (6.2 ± 0.3 $cm^2\ y^{-1}$). *Q. ilex* growth rates were significantly higher at SE and NW (9.5 ± 0.6 and 9.0 ± 0.4 $cm^2\ y^{-1}$, respectively) than at SW but still significantly lower than at NE, where BAI was the highest (18.9 ± 1.2 $cm^2\ y^{-1}$). BAI was higher for *F. sylvatica* than *Q. ilex* at all sites except NE. *Q. ilex* BAI at NE was similar to the average *F. sylvatica* BAI at SE, NW and NE and significantly higher than at SW site. The period of mature growth in which the BAI temporal trends were assessed differed between species and sites (Table 2). *F. sylvatica* BAI in the mature phase had a significantly negative trend at SW, a non-significantly negative trend at SE and a significantly positive trend at the two northern sites (NW and NE). *Q. ilex* BAI in the mature phase show positive significant trends at the western sites (SW and NW) and non-significant trends at the eastern sites (SE and NE). The different lengths of the mature growth period, however, could have affected these results. The analysis of the period when all chronologies reached mature growth (1987–2011) indicated that *F. sylvatica* BAI has recently tended to decrease at the southern sites (SW and SE). *Q. ilex* BAI at the two northern sites (NW and NE) has increased significantly. The other BAI chronologies had no significant trends during 1987–2011.

The correlations between RWI and climate for 1968–2011 were clearly species-specific. *F. sylvatica* had the highest correlations with temperature. The effect of maximum temperature on growth was negative in June and July of the year of the growth of the ring across all the studied sites, and there was also a negative carry-over effect of maximum temperatures from the previous summer (Fig. 4). Similar to

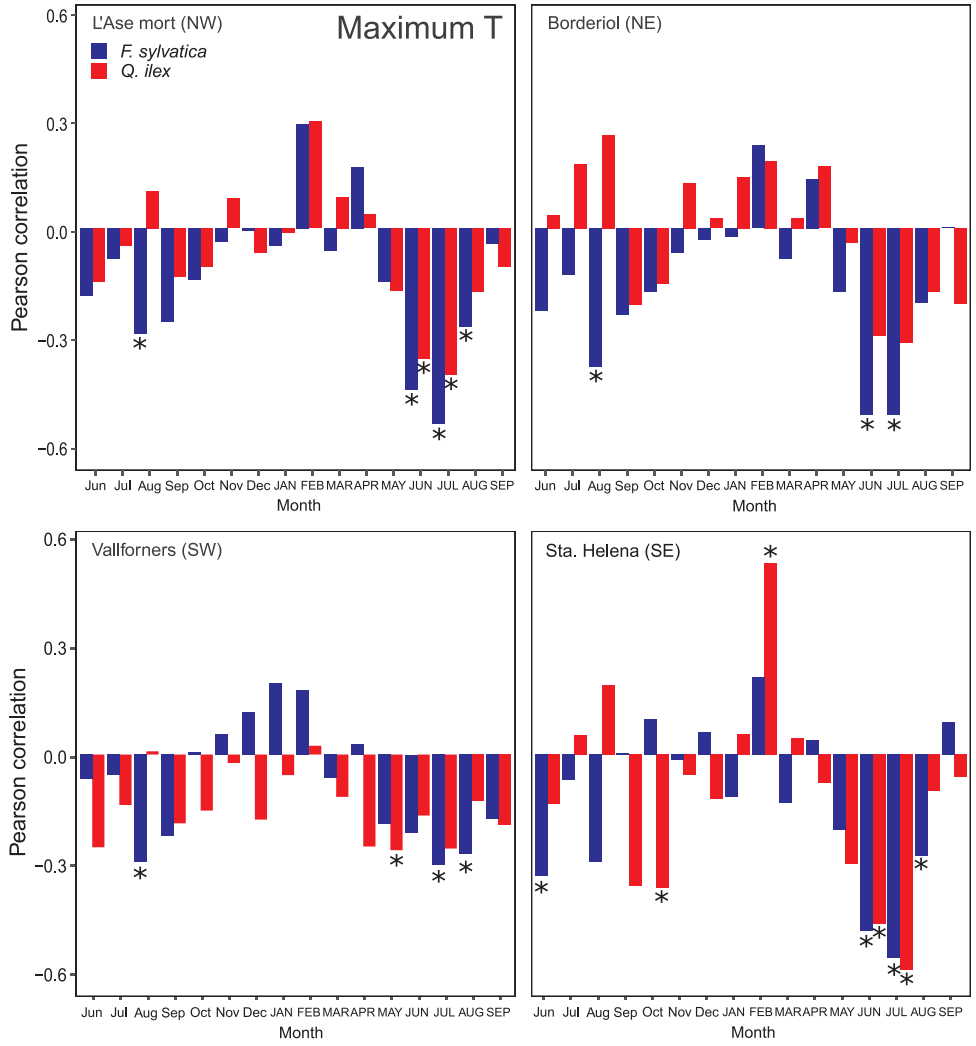

Fig. 4. Correlations between maximum temperatures and the ring-width index for *F. sylvatica* (blue bars) and *Quercus ilex* (red bars) at the four sites for the period 1968–2011. Significant correlations ($P < 0.05$) are indicated with asterisks. Months in lowercase letters correspond to the year prior to tree-ring formation, and months in uppercase letters correspond to the year of tree-ring formation.

temperature, early summer rainfall (June and July) had a positive effect on growth, with the exception of the SW site that only showed a positive correlation in August (Fig. 5). *F. sylvatica* tree-ring growth showed a clear positive correlation with foggy days in all the studied sites. This was true for the year of the growth of the ring (June and July) but also for the previous year (August and September) (Fig. 6). Because foggy days are correlated with summer rainfall and temperature (Fig. S3), summer correlations between growth and fog would be in fact caused by rainfall and temperature. But summer fog affected significantly *F. sylvatica* growth still when the variability explained by rainfall was removed (Fig. 7). On the other hand, once the variance in growth explained by maximum temperatures was removed, the effect of summer was non-significant. These patterns were common in all sites for *F. sylvatica*. The link between the effects of summer maximum temperatures and foggy days on growth is also clear for the summer of the year previous to tree-ring formation (Fig. S6).

The *Q. ilex* climate-growth relationships were more variable among the sites and differed substantially from those of *F. sylvatica* (Figs. 4–6 and S7). The negative effect of summer temperature was less consistent than for the deciduous trees, except in the SE site (Fig. 4). Minimum temperatures caused lower tree-ring growth only in the sites located at the southern part of the mountain range. In contrast to *F. sylvatica,* carry-over effects from the previous year temperatures were overall irrelevant. The effect of rainfall on growth for *Q. ilex* was slightly site-dependent, and mirrored that of *F. sylvatica* (Fig. 5). Even more site-dependent was the effect of summer foggy days, which was mostly significant only at the southern sites (SE and SW) and both in the year of the growth of the ring and the previous one. The SW site showed at the same time the highest correlations with fog and the lowest with rainfall. Overall, the partial correlations showed that the positive effect of fog on *Q. ilex* would be linked to some extent to higher rainfall occurring during foggy weather, especially in the northern sites. This is illustrated by the non-significant correlations observed between summer fog and growth when the variance explained by rainfall was removed (with the exception of the SE site) (Fig. 7). Still, the cooling effect of summer fog could have a more relevant role. Even if fog is significant when analyzed alone, this effect disappeared after removing the variance in growth explained by maximum temperature (Fig. 7 and Fig. S8).

4. Discussion

4.1. Decline in fog frequency and its effects on Mediterranean-temperate forest ecotones

We report a dramatic 62% decrease in fog frequency from the late 1960s to the present decade in a coastal Mediterranean mountain range. This represents a decrease in the annual number of foggy days

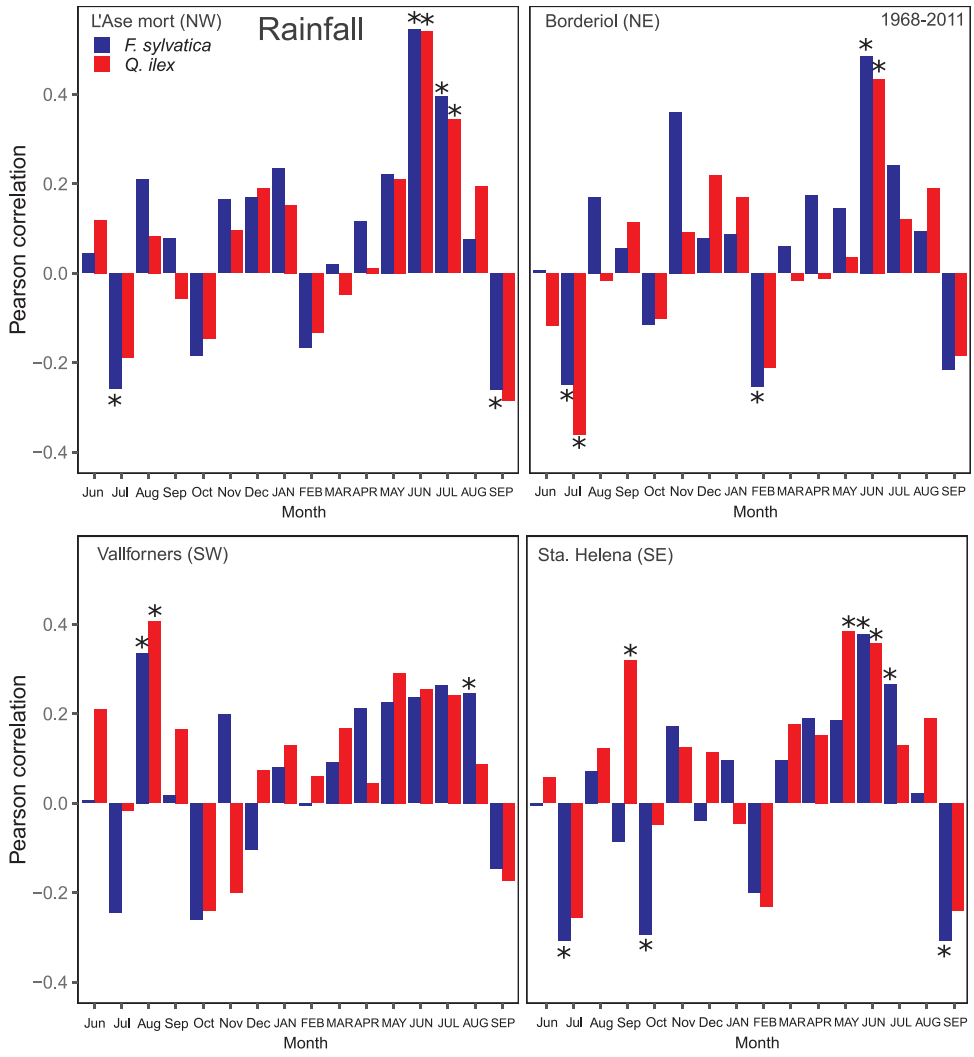

Fig. 5. Correlations between monthly rainfall and the ring-width index for *F. sylvatica* (blue bars) and *Quercus ilex* (red bars) at the four sites for the period 1968–2011. Significant correlations ($P < 0.05$) are indicated with asterisks. Months in lowercase letters correspond to the year prior to tree-ring formation, and months in uppercase letters correspond to the year of tree-ring formation.

from 231 to 87, concomitant with a warming trend of ca. 0.1 °C per decade since 1920 (Fig. 2). Accordingly, a significant decrease in air relative humidity in the last 20 years was measured in two other meteorological stations located in the same mountain range (Fig. S9). Multi-decadal decreases in fog frequency have been reported for regions with frequent advective fog (Johnstone and Dawson, 2010) but also at a continental scale in Europe (Vautard et al., 2009). Cloud height of upslope fog is predicted to increase in tropical regions as temperatures rise, with negative impacts on tropical montane cloud forests (Goldsmith et al., 2013; Still et al., 2009). A similar process may be occurring at the limit between Mediterranean and temperate biomes. The decrease in fog frequency in the Montseny Mountains may be due to an increase in cloud height caused by warmer temperatures. Indeed, fog frequency was correlated negatively with temperature and positively with rainfall, especially in summer (Fig. S3). The increase in cloud height caused by warmer temperatures may in turn have positive feedbacks on the warming trend at the local scale. Such feedbacks could account for the decrease in relative humidity on both the north- and south-facing slopes of the mountain range in the last two decades (Fig. S9). However, a significant increase in vapor-pressure deficit for the same period was only observed in the southern side of the mountain range (Fig. S9), which is more exposed to sea breezes (Panareda, 1979). The decrease in fog frequency indicated that this phenomenon may be more sensitive than temperature to climate change and clearly much more sensitive than rainfall. Fog immersion may contribute substantially to the water budgets of ecosystems by reducing evapotranspiration (Clark et al., 2014; Scholl et al., 2011). A reduction of fog events could therefore also indirectly affect the amount of water available for runoff and groundwater recharge in the already water-limited Mediterranean region.

Fog has traditionally been associated with the distribution of *F. sylvatica* and with the altitude of the Mediterranean-temperate ecotone in this mountain range (de Bolòs, 1983; Gutiérrez, 1988), thus we expected a strong effect of fog frequency on tree-ring growth, mostly for *F. sylvatica* at the southern sites. Indeed, fog was a primary climatic factor affecting radial growth at similar magnitudes than rainfall and temperature, especially in *F. sylvatica* (Fig. 6). Contrary to what we hypothesized, fog was relevant for *F. sylvatica* growth regardless of the site distance to the sea and exposure to its breezes. For this deciduous tree, the effect of fog was fairly independent of rainfall, as shown by partial correlations (Fig. 7). In addition, the positive effect of late summer fog in the year previous to the growth of the ring was not paralleled by the effect of rainfall (Fig. 5 and Fig. S10). This is in agreement with previous studies that reported the alleviation of drought stress by summer cloudiness in other rear-edge stands of *F. sylvatica* (Rozas et al., 2015). In fact, the effect of fog disappears when accounting for the variability

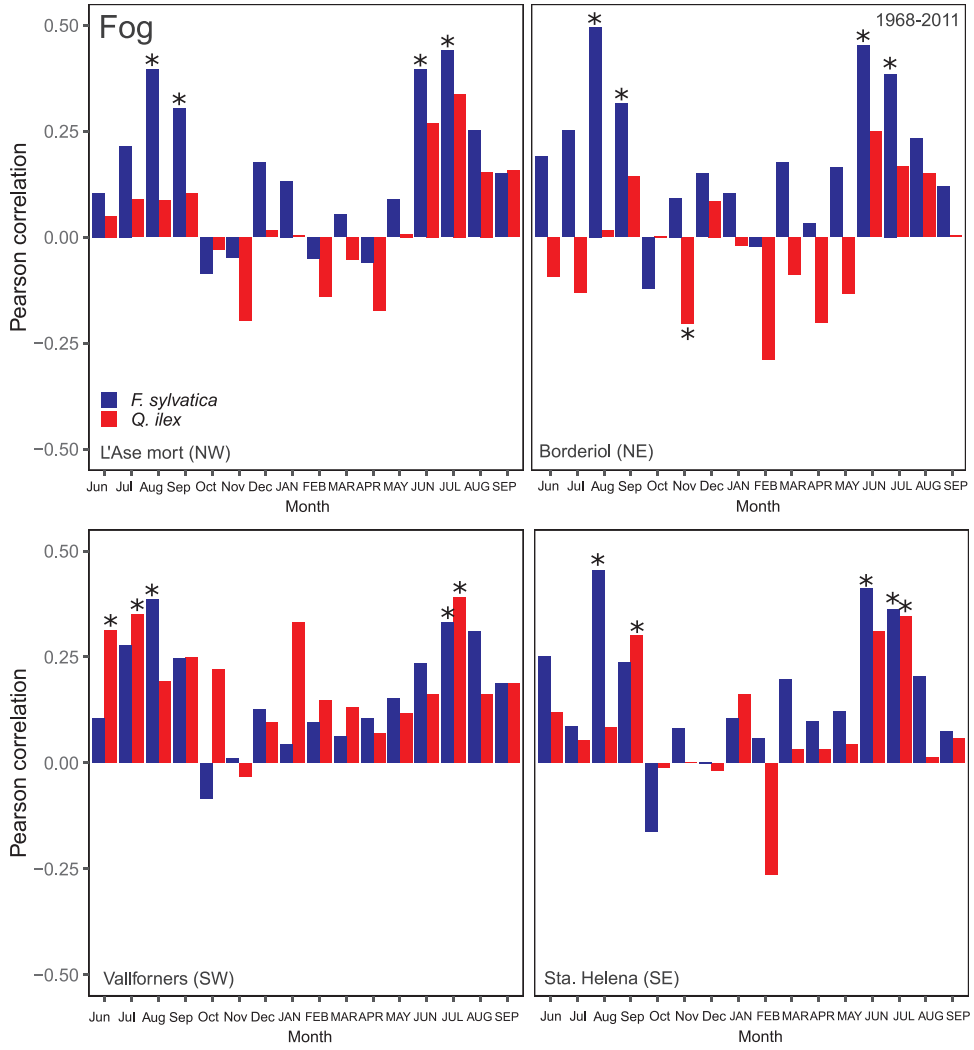

Fig. 6. Correlations between monthly foggy days and the ring-width index for *F. sylvatica* (blue bars) and *Quercus ilex* (red bars) at the four sites for the period 1968–2011. Significant correlations ($P < 0.05$) are indicated with asterisks. Months in lowercase letters correspond to the year prior to tree-ring formation, and months in uppercase letters correspond to the year of tree-ring formation.

caused by maximum temperatures in the summer of the growth (Fig. 7), but also in the previous one (Fig. S6). Overall, we provide evidence that fog can have beneficial effects on tree growth of this temperate deciduous species, and that this effect is mediated by a dampening of the negative effects of temperatures, rather than by an increased water input. Our results thus confirm that the distribution of *F. sylvatica* is linked to the presence of fog at the southern edge of its distribution, as it was suggested by bioclimatic observations made almost four decades ago (Panareda, 1979).

The effect of fog on the growth of *Q. ilex* was not as general as for *F. sylvatica* (Figs. 6 and 7). It was clearly stronger in the southern sites, which are more exposed to sea breezes. More importantly, fog effects were generally linked to positive effects of rainfall. Foggy and rainy conditions are synchronous during cyclonic situations (Corell Custardoy et al., 2014). Since most of the correlations with fog disappeared after removing the variability explained by rainfall (Fig. S11), fog's significant effect on *Q. ilex* growth could be in fact produced by its coincidence in time with rainfall. Despite *Q. ilex* growth was more independent from fog than that of *F. sylvatica*, their positive growth-fog correlations shared probably the same mechanism, buffering from warm summer temperatures (Fig. 7). In the long term, the decrease in fog frequency would eventually impact less the growth of *Q. ilex* than that of *F. sylvatica*. This is also supported by the lower frequency of fog events and scarcer amounts precipitated in the lower altitude areas dominated by the evergreen Mediterranean *Q. ilex* (Corell Custardoy et al., 2014).

4.2. Growth sensitivity to climate and long-term trends

The sensitivity of *F. sylvatica* growth to climate was very similar between the studied sites, except for the more isolated Vallforners population (SW). Growth was mainly determined by the water balance in early summer (positive effects of rainfall and negative effects of temperature), in agreement with previous studies in the area (Gutiérrez, 1988; Jump et al., 2007) and distribution-wide analyses (Hacket-Pain et al., 2016). Minimum temperatures in February also had a positive effect on growth, which could be attributed to an earlier leaf unfolding and cambial reactivation during warm late winters (Čufar et al., 2008). Although *F.* sylvatica radial growth can be negatively affected by late frosts (Dittmar et al., 2006), we did not find any effect of minimum temperatures in April or May, the time of leaf unfolding (Fig. S7). Thus, *F. sylvatica* may be less vulnerable to late frosts at the southern, warmer edge of its distribution. Maximum temperatures late in the previous summer had negative effects on growth everywhere but in the NW site, which has been pointed out previously (Cavin and Jump, 2017).

Q. ilex growth was slightly less sensitive than *F. sylvatica* growth to climate, except at the more exposed southern site (SE). Rainfall in early summer can increase growth, and high temperatures in July can

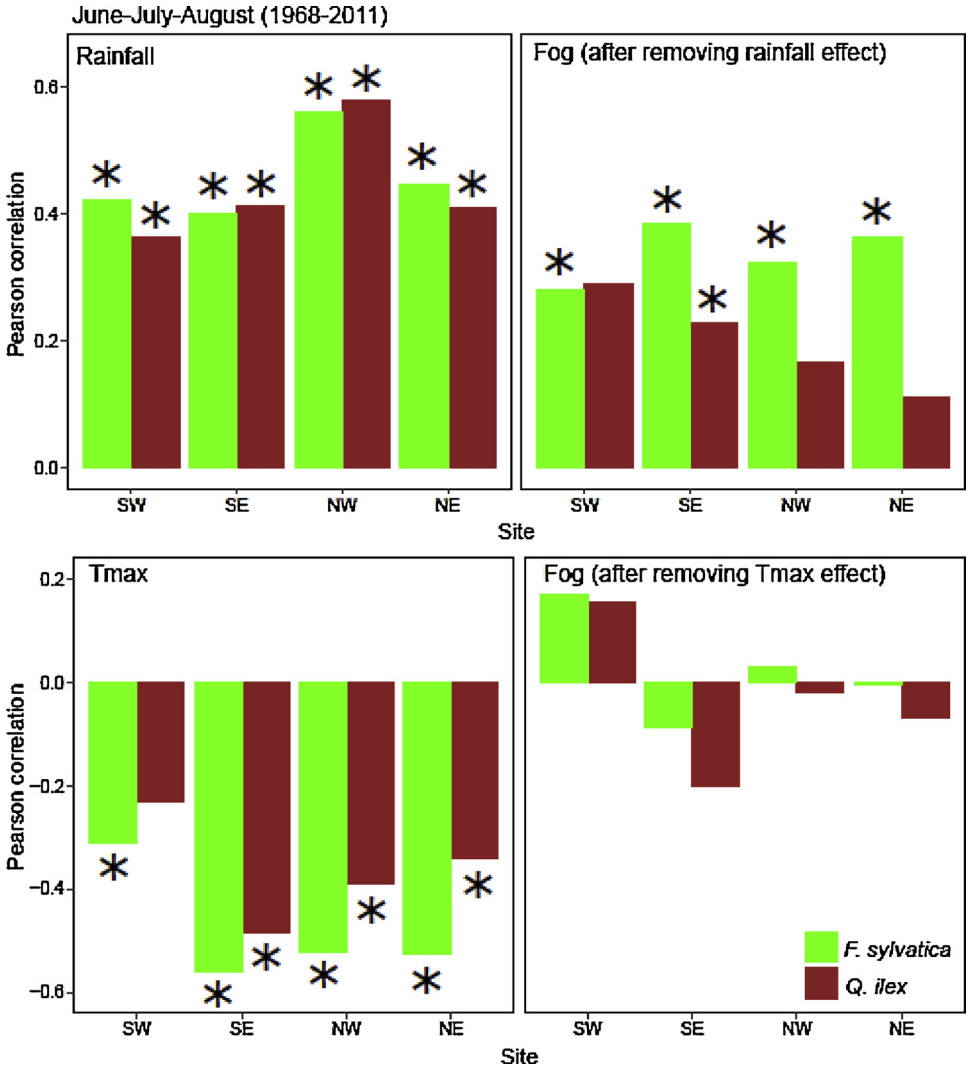

Fig. 7. Seasonal (three-month) climate-growth partial correlations. The two left panels show the correlations with a primary variable (top, rainfall; bottom, maximum temperature) for each site and tree species. The two right panels show the partial correlations of foggy days with growth after removing the effect of the primary variables shown in the left panels. The three-month period (from June- to August) corresponds to the year of tree-ring formation. Significant Pearson correlations ($P < 0.05$) are indicated with asterisks. The rest of explanations are as in Fig. 6.

decrease growth, as has been observed in other Iberian *Q. ilex* populations (Gea-izquierdo et al., 2011; Gea-Izquierdo et al., 2009; Gimeno et al., 2012). Radial growth in *Q. ilex* has a quiescent period of cambial activity in the summer peak (Camarero et al., 2015a, 2015b; Gutiérrez et al., 2011; Montserrat-Martí et al., 2009; Sánchez-Costa et al., 2015). July temperature and rainfall could trigger the onset of this quiescence, the duration of which has a direct effect on growth and carbon uptake (Lempereur et al., 2015). The presence of fog may thus decrease drought stress and delay the summer cessation of growth. Summer fog, however, had a positive effect only at the southern sites, which are more exposed to sea breezes. Foggy days during the November prior to growth, though, had a negative effect on the growth of the northern populations of *Q. ilex*. Active carbon assimilation can still occur in November, although trees do not usually grow due to low temperatures (Gutiérrez et al., 2011), so light-limiting foggy conditions would have carry-over effects mediated by lower rates of photosynthesis and replenishment of carbon reserves. The sites closer to the sea showed stronger effects of fog in *Q. ilex* than more continental sites, but this was not observed in *F. sylvatica*. This implies that fog patterns may not completely differ between the southern and northern sides of the mountain range. It seems rather that it is the interaction of fog with temperature effects on *Q. ilex* growth that is more spatially variable.

Q. ilex had lower growth rates at all sites except NE, even though *F. sylvatica* growth was more sensitive to summer drought and heat, as shown by its stronger growth-climate relationships. NE, however, was the only site at which the mean diameters of the two species were similar (Table 1). Likewise, the *F. sylvatica* trees were slightly older and larger than the *Q. ilex* trees at the other three sites, which could account for the difference in growth despite their higher sensitivity to summer drought and heat. The stands of *F. sylvatica* nevertheless had growth rates similar to those of other populations along the southern edge of its distribution (Cavin and Jump, 2017), but the rates were clearly lower than in stands at higher altitudes or wetter sites within the same mountain range but not in the Mediterranean-temperate ecotone (Jump et al., 2006). *Q. ilex* growth rates, though, were two- to ten-fold higher at all sites than in other populations (Granda et al., 2013; Barbeta et al., 2013; Lempereur et al., 2015; Camarero et al., 2015b). *F. sylvatica* in this forest ecotone therefore grows at the lowest margin of its species potential, whereas *Q. ilex* growth rates were much higher than the species average, suggesting very good climatic conditions for growth. Mature growth was more variable among sites for *Q. ilex* than *F. sylvatica*. *Q. ilex* growth rates were three-fold higher at NE than SW, whereas *F. sylvatica* growth rates were less than two-fold higher. The wider distribution of *Q. ilex* in the region suggests that it is less sensitive

to topography (Barbeta and Peñuelas, 2016). *Q. ilex* growth rates, however, were more strongly influenced by topography than *F. sylvatica* growth rates as they were more variable among sites. The sensitivity of *Q. ilex* to climate appeared to more site-dependent than that of *F. sylvatica*, leading to the larger spatial variability in observed in the growth rates of *Q. ilex*.

4.3. Concluding remarks

Early-summer rainfall and maximum temperatures were the most important factors determining *F. sylvatica* growth, but summer fogs had important complementary positive effects, which were clearly mediated by their impact on summer temperature (Fig. 7). Long-term reduced fog frequency may thus exacerbate tree drought stress by the end of the growing season, when the accumulated soil-water deficit is higher. The decrease in fog observed since the late sixties has not produced yet a general decline of *F. sylvatica* growth at this area located at the southern-most limit of its distribution. This is surprising given that the sensitivity of the species to summer drought was likely the most relevant factor determining tree growth, and summer tree water stress must have increased given the reported climatic records. Therefore, *F. sylvatica* forests were not pervasively negatively affected by warming temperatures, except at the most extreme sites, which is in agreement with a previous study assessing long-term growth trends (Jump et al., 2006). The most extreme sites correspond to the lowest altitudes (940–1040 m reported by Jump et al. (2006)) or to isolated, marginal populations (the SW *F. sylvatica* stand in the present study). These populations would also suffer from increased inbreeding and thus reduced genetic diversity that may impair their persistence and evolutionary potential in the face of environmental changes (Jump and Peñuelas, 2006). Even if growth trends of *F.* sylvatica did not decline in response to a changing climate, this species may suffer from competition with the evergreen *Q. ilex* in the long term. *Q. ilex* generally had more positive growth trends (Fig. 3, Table 2), which, together with the absence of growth limitation by winter cold, places this species as a strong competitor for *F. sylvatica* in this forest ecotone. Competition between deciduous and evergreen hardwood trees would become even more detrimental for deciduous trees if the predictions for temperature trends are confirmed. Furthermore, the decrease in fog immersion, especially in summer, will mainly benefit *Q. ilex*, because its growth is less dependent on this phenomenon than *F. sylvatica*.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agrformet.2018.10.020.

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